

The fossil record of freshwater Gastropoda – a global review

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ABSTRACT

Gastropoda are an exceptionally successful group with a rich and diverse fossil record. They have conquered land and freshwater habitats multiple times independently and have dispersed across the entire globe. Since they are important constituents of fossil assemblages, they are often used for palaeoecological reconstruction, biostratigraphic correlations, and as model groups to study morphological and taxonomic evolution. While marine faunas and their evolution have been a common subject of study, the freshwater component of the fossil record has attracted much less attention, and a global overview is lacking. Here, I review the fossil record of freshwater gastropods on a global scale, ranging from their origins in the late Palaeozoic to the Pleistocene. As compiled here, the global fossil record of freshwater Gastropoda includes 5182 species in 490 genera, 44 families, and 12 superfamilies over a total of ~340 million years. Following a slow and poorly known start in the late Palaeozoic, diversity slowly increased during the Mesozoic. Diversity culminated in an all-time high in the Neogene, relating to diversification in numerous long-lived (ancient) lakes in Europe. I summarise well-documented and hypothesised freshwater colonisation events and compare the patterns found in freshwater gastropods to those in land snails. Furthermore, I discuss potential preservation and sampling biases, as well as the main drivers underlying species diversification in fresh water on a larger scale. In that context, I particularly highlight the importance of long-lived lakes as islands and archives of evolution and expand a well-known concept in ecology and evolution to a broader spectrum: scale-independent ecological opportunity.

Key words: biodiversity, colonisation, ecological opportunity, long-lived lakes, non-marine Mollusca, palaeogeography, preservation.

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I. INTRODUCTION

Phylum Mollusca is one of the most speciose groups in the animal kingdom. Estimates for species richness range from 70,000 to 120,000 described valid species, and up to 200,000 including undescribed species [Rosenberg, 2014; Bouchet *et al.* (2016), and references therein]. A latest query of the online database MolluscaBase lists 85,852 accepted extant species as of 16 May 2023 (MolluscaBase eds, 2023).

Mollusca are an extraordinarily successful group, not only reflected in their high extant diversity but also their wide geographic and ecological distribution. Mollusca are globally distributed and have conquered nearly all types of environments, from marine to freshwater to terrestrial; they occur from deep-sea trenches to mountain tops, and from tropical forests to desert environments (Leal & Harasewych, 1999; Strong *et al.*, 2008; Haszprunar & Wanninger, 2012; Gittenberger *et al.*, 2021; MolluscaBase eds, 2023). The majority of species (~50,500) are marine or brackish-water species, ~28,400 are terrestrial snails, and ~6700 are freshwater gastropods and bivalves (MolluscaBase eds, 2023).

The success of Mollusca today is rooted in a long and rich fossil record that dates back to the early Cambrian, ~540 million years (Myr) ago (Wanninger & Wollesen, 2019). Their evolutionary origins probably reach even into the terminal Ediacaran, although no Ediacaran fossil material can yet be unambiguously attributed to molluscs (Vinther, 2015; Zhuravlev & Wood, 2018; Wanninger & Wollesen, 2019). Similar to their extant diversity, marine molluscs make up the majority of species richness in the fossil record. Fossil marine molluscs are comparatively well studied and patterns in their diversity through deep time are well known (e.g. Wagner, 1995; Dmitriev & Nevesskaja, 2006; Nevesskaya, 2008; Vinarski, Bondarev & Markov, 2011; Mondal & Harries, 2016; Rineau, Smyčka & Storch, 2022).

Freshwater molluscs have received considerably less attention. With 6658 described extant species (MolluscaBase eds, 2023), representing 7.8% of mollusc total diversity, they are still a relatively diverse group considering that their freshwater habitats occupy less than 1% of the planet's surface (Strayer & Dudgeon, 2010; Darwall *et al.*, 2020). Freshwater habitats and molluscs provide important ecosystem services that sustain human populations in terms of freshwater supply, nutrition, and health (Green *et al.*, 2015; EEA, 2019).

With 7558 valid species, the fossil record of freshwater molluscs is at a similar magnitude as today's diversity (MolluscaBase eds, 2023). Fossil freshwater molluscs have been found on all continents including Antarctica

(Taylor, 1988; Martínez *et al.*, 2020). The oldest ascertained freshwater representatives are bivalves and date back to the Devonian (Taylor, 1988). A much more diversified record is known from Carboniferous and Permian strata, although none of the Palaeozoic freshwater Bivalvia are attributable to modern families (Trueman & Weir, 1946–1968; Taylor, 1988; Skawina & Dzik, 2011; Silantiev, 2018). The Palaeozoic record of freshwater gastropods is much less certain and poorly resolved. Earliest records may also date back into the Devonian, followed by a few species known from Carboniferous and Permian deposits, yet their systematic placement and even their status as freshwater fossils is usually uncertain (Solem & Yochelson, 1979).

Freshwater colonisation took place multiple times independently in molluscs. Accounting for both fossil and recent molluscs, at least 20 clades of gastropods and 17 of bivalves contain freshwater taxa (Vermeij & Dudley, 2000; Miller & Labandeira, 2002; Vermeij & Wesselingh, 2002). Strong *et al.* (2008) considered there to be 33–38 independent freshwater lineages among extant Gastropoda alone.

In the fossil record, freshwater molluscs are important indicators for palaeoecological conditions (e.g. Van Damme & Pickford, 1994; Miller & Tevesz, 2001; Wesselingh *et al.*, 2002; Nishida *et al.*, 2013; Van Bocxlaer, 2020) and some evolutionary lineages qualify as stratigraphic markers (e.g. Taktakishvili, 1967; Hartman, 1998; Magyar & Geary, 2012; Neubauer, Harzhauser & Kroh, 2013; Mandic *et al.*, 2015; Lubenescu, 2016). They have also been used to study the patterns, modes, and processes of evolution and biodiversity build-up and decline (e.g. Taktakishvili, 1967; Neubauer *et al.*, 2013, 2014a, 2015b, 2021, 2022a,b; Rasser & Covich, 2014; Neubauer & Harzhauser, 2022), or to reconstruct palaeobiogeographic relationships (Taylor, 1988; Watters, 2001; Wesselingh, 2007; Harzhauser & Mandic, 2008; Neubauer *et al.*, 2015c, 2016c).

Despite a rich and long fossil record of freshwater Gastropoda, paired with a long research tradition, there are relatively few large-scale overviews in the literature. The first comprehensive assessment was made by Wenz (1923–1930), who provided a systematic catalogue of all fossil species of land and freshwater gastropods from the Cenozoic (mostly of Europe) known until then, along with systematic revisions and extensive synonymies. In a similar manner, Henderson (1935) provided a catalogue of North American species from Mesozoic and Cenozoic deposits. Wenz (1938–1944) and Zilch (1959–1960) published a systematic account of living and fossil non-marine Gastropoda together with geographic and stratigraphic information of all genera. Taylor (in Gray, 1988)

listed and discussed the first appearances of higher taxa of freshwater molluscan groups. In a second work, he discussed the geographic distributions of certain groups in a palaeobiogeographic context (Taylor, 1988). Neubauer *et al.* (2014b) provided a systematically and taxonomically updated list of all Neogene species from Europe. On a smaller geographic and taxonomic scale, Salvador *et al.* (2018) reviewed the fossil record of Cretaceous to Neogene Hygrophila and Eupulmonata of South America. Haszprunar (2014, 2022), Neubauer (2016), and Neiber & Glaubrecht (2019a) produced nomenclators of all available fossil and recent genus and species names of Valvatidae, Melanopsidae, and Paludomidae, respectively. Recently, the global fossil record of Lymnaeidae was summarised by Neubauer (2023) along with an assessment of the family's diversity and geographic distribution through time.

Herein, I present the first complete survey of the world-wide fossil record of freshwater Gastropoda, from their roots in the late Palaeozoic to the Pleistocene, based on state-of-the-art systematic attributions and an account of diversity across space and time. Continental diversity through time is illustrated using palaeogeographic reconstructions. Further, I summarise and discuss freshwater colonisation events, compare these to patterns in land snails, and conclude with a broader discussion on the non-uniform distribution of diversity and its various causes.

II. MATERIALS AND METHODS

This review includes fossil-only freshwater taxa from the late Palaeozoic (Carboniferous) to the Quaternary (Pleistocene); extant species that have a fossil record are not included. Data derived from two sources. A large part is provided by the species occurrences collected in the course of recent publications (Neubauer *et al.*, 2015b,c, 2021, 2022a,b), representing the most complete occurrence data sets for Europe and North America for the Mesozoic and Cenozoic. For all other species, data on taxonomy, distribution and fossil ages were gathered from the literature (original descriptions and revisions) and made available online *via* MolluscaBase (MolluscaBase eds, 2023). That database includes all known fossil non-marine species together with the latest published systematic position and taxonomic status. This second data set contains a largely complete set of fossil age ranges for the valid species as well as comprehensive distribution data, especially for southern hemisphere continents and Asia where the data mainly derive from type localities. Distributions are illustrated in the form of Biodiversity Information Standards (historically known as the Taxonomic Databases Working Group, TDWG) polygons (Brummitt, 2001). A major geographic bias is unlikely considering that most species are only known from their type localities or small geographic regions. This is both a function of the comparatively poor fossil record and the geographically restricted nature of freshwater bodies. Hence, although the data set may not provide exhaustive

distribution data for all taxa, the chosen polygon-based approach provides a good approximation of overall species distribution.

Data from the two sources were combined and filtered for freshwater representatives, following habitat assignments in MolluscaBase as well as the literature (e.g. Strong *et al.*, 2008). Oligohaline species [inhabiting salinities up to 5‰ (Strydom, Whitfield & Wooldridge, 2003); e.g. including several species of Hydrobiidae] were included, while mesohaline taxa (5–18‰) were not. Largely amphibious to brackish-water groups such as Assimineidae, Ellobiidae, Potamididae, and most Truncatellidae were excluded, as were most Neritidae; only those genera with clear affinity to fresh water or oligohaline settings were included. Junior synonyms were matched with their valid names to update distribution and age records; similarly, subspecies were matched with their parent species. Uncertain names (*nomina dubia* and *taxa inquirenda*) were excluded from the analyses, while those that represent true species but are invalid or unavailable for nomenclatural reasons (e.g. unreplaced junior homonyms or taxa published in electronic format without fulfilling the requirements of the International Code of Zoological Nomenclature) were included. This enabled inclusion of 171 names published in a comprehensive monograph on Chinese Cenozoic faunas (Youluo, 1978) that is not available in the sense of the Code because no author is provided (*Youluo* means 'editorial group'; Haszprunar, 2022). Generally, this review provides an uncritical summary of the current knowledge; while several uncertainties are discussed, no revisions or taxonomic decisions are made. The list of included freshwater/oligohaline species is provided as online Supporting Information in Table S1.

Fossil ages were linked to the International Chronostratigraphic Chart (v. 2023-04; Cohen *et al.*, 2013). The temporal units chosen for this review are the Epoch, for total and group diversity through time, and the Period, for large-scale reconstructions of palaeobiogeography. Distributions were matched to TDWG level-4 polygons, representing countries or higher administrative units of larger countries, to illustrate species richness per region. Islands smaller than 500 km² were excluded from the maps. Fifty-nine species lacked age information or were excluded because the available information was of too coarse a scale (i.e. age ranges exceeding the Period). For distributions, 53 species lacked information or their TDWG polygons were of low resolution, i.e. greater regions or large countries (level 3 or level 2). Data for the palaeogeographic reconstructions are derived from Kocsis & Scotese (2021). The attribution of polygons to continents follows the TDWG scheme (level-1 polygons; Brummitt, 2001), with the exception that the Caucasus region and East Aegean islands are attributed to Europe. Continent delimitation in the fossil record is based on the present-day political situation. In selected cases, this may not accurately reflect palaeogeography (e.g. in the case of the Indian subcontinent), but the generally low number of taxa from such regions does not introduce a serious bias. Data for

distributions and ages are provided in Tables S2 and S3 respectively.

The diversity data underlying the graph of colonisation events is based on a MolluscaBase query of all extant accepted gastropod species (MolluscaBase eds, 2023). Data were binned into three systematic levels following Bouchet *et al.* (2017) to assess the relative diversity of higher taxa. Fossil species were not considered in this particular analysis, since the fossil record of marine species in MolluscaBase is incomplete. Moreover, there are no higher level fossil-only clades that include non-marine gastropods.

All analyses and maps were generated in R v. 4.1.2 (R Core Team, 2021), using the packages *dplyr* v. 1.0.8 (Wickham *et al.*, 2022), *tidyverse* v. 1.3.1 (Wickham, 2022), *rgdal* v. 1.5-28 (Bivand, Keitt & Rowlingson, 2021), *sf* v. 1.0-6 (Pebesma, 2018), *sp* v. 1.4-6 (Bivand & Pebesma, 2013), *ggplot2* v. 3.3.5 (Wickham *et al.*, 2021), *smoothr* v. 0.2.2 (Strimas-Mackey, 2021), and *units* v. 0.8-0 (Pebesma, Mailund & Hiebert, 2016).

III. A GLOBAL REVIEW OF THE FOSSIL RECORD

The Carboniferous–Pleistocene global fossil record of freshwater/oligohaline Gastropoda contains 12 superfamilies, 44 families, 490 genera, and 5182 species (Fig. 1, Table 1). Inclusion of all subspecific ranks (subspecies, varieties, forms, and subvarieties) and unaccepted names (junior synonyms, homonyms, unjustified emendations, *taxa inquirenda*, and *nomina dubia*) increased this number to 6923. In addition, there are 38 *nomina nuda* in the data set.

Truncatelloidea are by far the most abundant group with 1906 species, followed by Lymnaeoidea (1142 species), Cerithioidea (900 species), Viviparoidea (600 species), and Neritoidea (241 species) (Fig. 1). Patterns in diversity across geological time for each superfamily are shown in Fig. S1. On the family level, Hydrobiidae (Truncatelloidea) are the dominant group (1102 species), followed by Viviparidae (Viviparoidea) (594 species), Planorbidae (Lymnaeoidea) (577 species), Melanopsidae (Cerithioidea) (394 species), and Lymnaeidae (Lymnaeoidea) (371 species) (Fig. 1, Table 1). Patterns in diversity across geological time for each family are shown in Fig. S2.

In the following, I discuss the fossil record of each stratigraphic period, from the Carboniferous to the Pleistocene, and use palaeogeographic maps and charts to illustrate species diversity across major systematic groups. I discuss the first occurrences of superfamilies and families (Table S4) and notable centres of diversity. The oldest stratigraphic records of families and superfamilies indicated herein must, however, be considered with caution. Despite the paucity of morphological characters associated with many freshwater shells, often coupled with poor preservation (especially for material from Mesozoic strata), many species were classified into modern genera and families in the past, even where placement in a superfamily was poorly

supported. Moreover, many fossils have not been identified to the species level but were left in open nomenclature; because of their taxonomic uncertainty, these are not considered herein.

(1) The origin of freshwater gastropods: the Palaeozoic

(a) Carboniferous

Little is known about the roots of freshwater gastropods in the Palaeozoic (Fig. 2, Table S4). Occurrences are patchy, taxon attributions to genera and even higher systematic groups are problematic, and even their freshwater status is uncertain in several cases (Yen, 1949a; Solem & Yochelson, 1979; Taylor, 1988). Russell (1947) recorded a 'viviparid-like form' of gastropod from Devonian strata of Quebec, but the accompanying fauna of eurypterids and modiomorphid bivalves rather indicates a marine environment.

Four supposed freshwater species are known from the Carboniferous. From the early Carboniferous, three species attributed to Hydrobiidae (Viséan stage), Pleuroceridae (probably Viséan), and Viviparidae (stage uncertain) have been reported from Great Britain (Garwood, 1922; Cox, 1927; Yen, 1949a; Solem & Yochelson, 1979) (Fig. 3). A species classified in Melanopsidae was reported by Fischer von Waldheim (1837) from strata attributed today to the Myachkovian regional stage (Late Moscovian; Mirantsev & Rozhnov, 2012) of Moscow region. None of these family placements are reliable, but poor preservation and lack of features impedes revision. They are therefore not considered herein as true first occurrences.

(b) Permian

Only four species have been described from Permian strata (Figs 2 and 3). Ludwig (1861) reported two species placed in Viviparidae and Planorbidae from the early Permian (Kungurian) of eastern European Russia. An additional supposed viviparid was listed by Geinitz (1861) from Saxony in eastern Germany (probably early Permian following the stratigraphy of LÖcse *et al.*, 2020). All three species were considered doubtful by Cox (1953). Further 'hydrobiid'-type taxa have been reported from the early Permian of Brazil (Runnegar & Newell, 1971; Solem & Yochelson, 1979).

Cox (1953) described a species classified in Hydrobiidae from the Karroo beds of Zimbabwe. Originally considered late Permian, the Lower Beaufort Group ['K5 subdivision (...), most probably the *Tapinocephalus* Zone'] Cox (1953, p. 201) attributed the finds to probably corresponds to the middle Permian following modern stratigraphic concepts (Lanci *et al.*, 2013; Day *et al.*, 2022). Finally, also from the Lower Beaufort Group, Rossouw (1970) reported a large, unidentified freshwater gastropod from South Africa. As for the Carboniferous taxa, none of the alleged systematic attributions of Permian taxa are here considered as first occurrences.

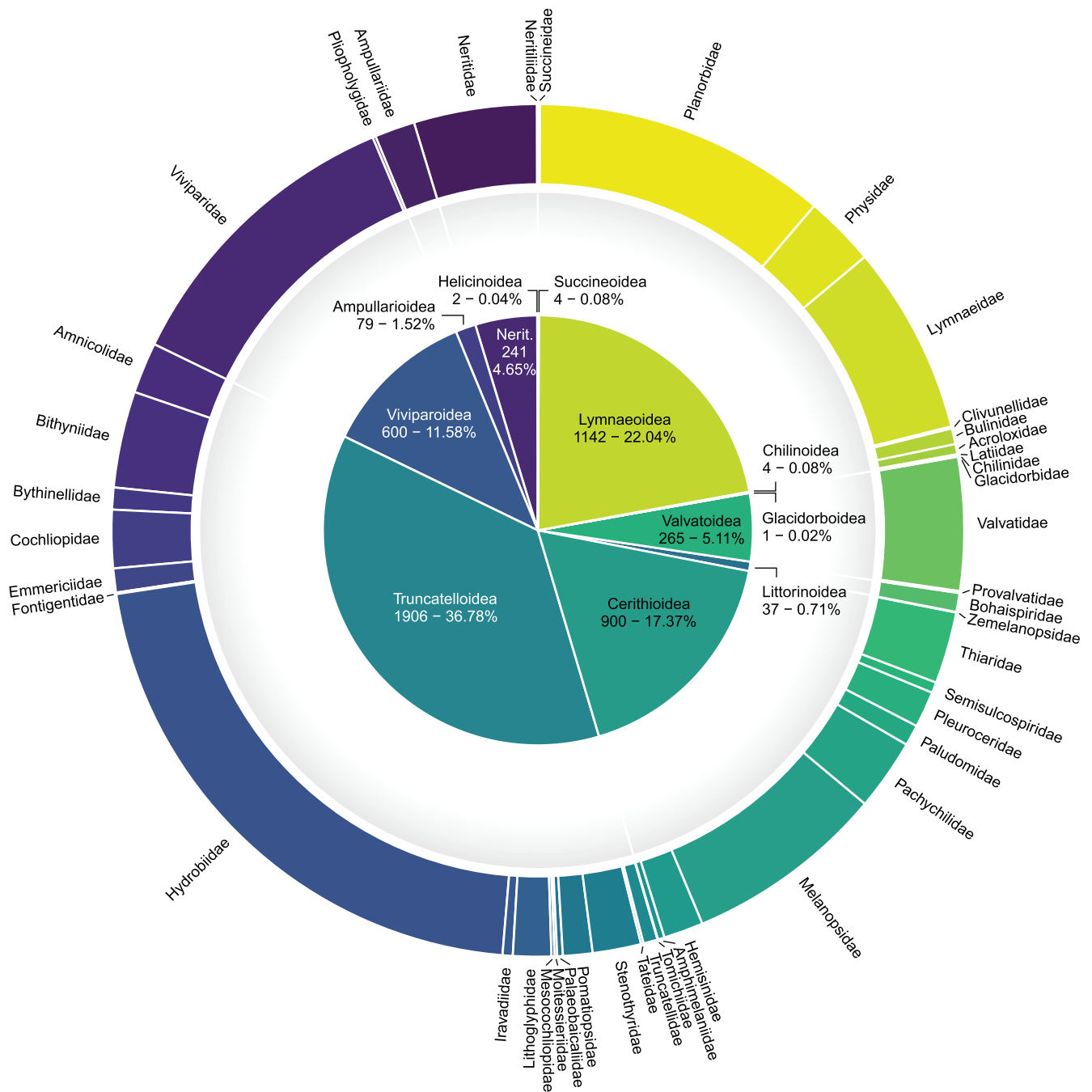


Fig. 1. Total species diversity of fossil freshwater/oligohaline gastropod superfamilies (inner pie chart: number of species – percentage) and families (outer donut chart). Superfamily systematic order follows Bouchet *et al.* (2017); families within each superfamily are ordered alphabetically.

(2) A slow but steady diversification: the Mesozoic

(a) Triassic

Global species diversity remained low throughout the Triassic and Jurassic (Figs 2 and 4). The earliest Mesozoic record of putative freshwater Gastropoda derives from the Early Triassic of China (Guo & Wei, 1984) (Figs 2 and 4). A single species from the Caiyuanzi (= Jiucayuan) Formation of

Xinjiang is attributed to the genus *Hydrobia* (family Hydrobiidae). However, the small, smooth shell without diagnostic features precludes classification even to the family level. The uncertainty of this attribution is enhanced by the complete absence of any other freshwater gastropod from the Early or Middle Triassic. If correctly identified, this record could link late Palaeozoic finds attributed to Hydrobiidae (Cox, 1927, 1953; Solem & Yochelson, 1979) to Late Triassic occurrences.

Table 1. Number of fossil freshwater/oligohaline species per gastropod family across geological time. See Fig. 1 for a graphical representation of these data. Superfamily systematic order follows Bouchet *et al.* (2017); families within each superfamily are ordered alphabetically. Four species of truncatelloids (genus *Avardaria*) are currently ‘unassigned’, and one genus (*Eocryphispira*) is entirely without placement (Gastropoda *incertae sedis*).

Superfamily	Family	Number of species
Helicinoidea	Neritiliidae	2
Neritoidea	Neritidae	241
Ampullarioidea	Ampullariidae	79
Viviparoidea	Pliopholygidae	6
Viviparoidea	Viviparidae	594
Truncatelloidea	Amnicolidae	100
Truncatelloidea	Bithyniidae	189
Truncatelloidea	Bythinellidae	43
Truncatelloidea	Cochliopidae	114
Truncatelloidea	Emmericiidae	47
Truncatelloidea	Fontigentidae	3
Truncatelloidea	Hydrobiidae	1102
Truncatelloidea	Iravadiidae	20
Truncatelloidea	Lithoglyphidae	75
Truncatelloidea	Mesocochliopidae	6
Truncatelloidea	Moitessieriidae	5
Truncatelloidea	Palaeobaicaliidae	11
Truncatelloidea	Pomatiopsidae	58
Truncatelloidea	Stenothyridae	95
Truncatelloidea	Tateidae	5
Truncatelloidea	Tomichiidae	1
Truncatelloidea	Truncatellidae	28
Truncatelloidea	‘unassigned’	4
Cerithioidea	Amphimelaniidae	13
Cerithioidea	Hemisinidae	78
Cerithioidea	Melanopsidae	394
Cerithioidea	Pachychilidae	140
Cerithioidea	Paludomidae	41
Cerithioidea	Pleuroceridae	71
Cerithioidea	Semisulcospiridae	21
Cerithioidea	Thiaridae	141
Cerithioidea	Zemelanopsidae	1
Littorinoidea	Bohaispiridae	37
Valvatoidea	Provalvatidae	4
Valvatoidea	Valvatidae	261
Glacidorboidea	Glacidorbidae	1
Chilinoidea	Chiliniidae	3
Chilinoidea	Latiidae	1
Lymnaeoidea	Acroloxidae	20
Lymnaeoidea	Bulinidae	31
Lymnaeoidea	Clivunellidae	4
Lymnaeoidea	Lymnaeidae	371
Lymnaeoidea	Physidae	139
Lymnaeoidea	Planorbidae	577
Succineoidea	Succineidae	4
Gastropoda <i>incertae sedis</i>		1
Total		5182

The Late Triassic witnesses the appearance of several groups in the fossil record (Table S4). Amnicolidae, Valvatidae, and Viviparidae appeared in North America (Yen, 1951a) and Valvatidae and Planorbidae in China

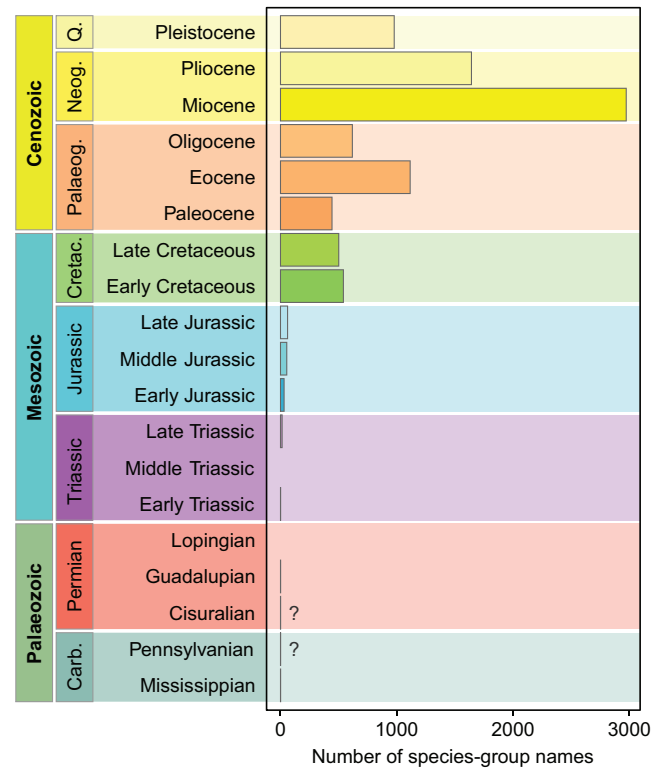


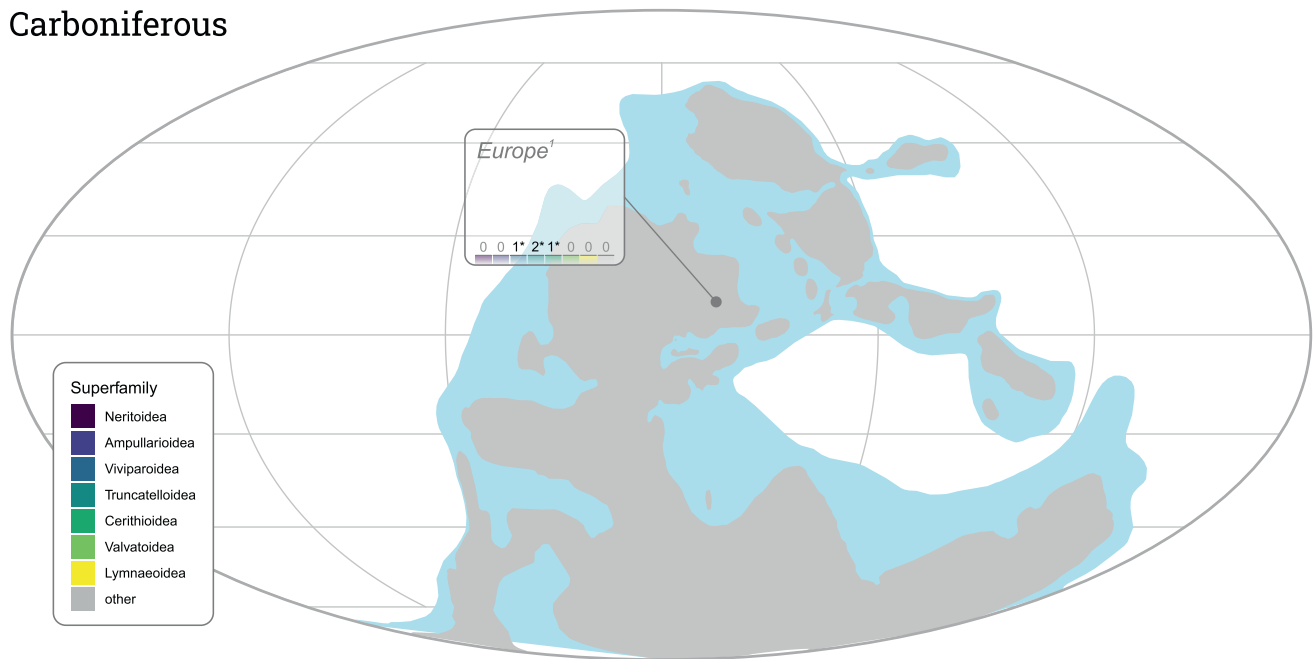
Fig. 2. Species diversity of freshwater/oligohaline gastropods across stratigraphic epochs. Question marks indicate records based on *taxa inquirenda*, some of which may constitute potential first occurrences of higher clades. Colours follow the International Chronostratigraphic Chart. For superfamily- and family-level charts see Figs S1 and S2 respectively. Carb., Carboniferous; Cretac., Cretaceous; Palaeog., Palaeogene; Neog., Neogene; Q., Quaternary.

(Guo, Yu & Pan, 1982; Guo & Wei, 1984). As for Hydrobiidae, the families Viviparidae and Planorbidae had been putatively documented from upper Palaeozoic strata (Ludwig, 1861; Garwood, 1922; Cox, 1927; see Section III.1.b). The extensive stratigraphic gap of several tens of millions of years between the Carboniferous/Permian [see Cox (1953) for a discussion of the Permian taxa recorded by Ludwig (1861)] and the Late Triassic strata casts doubt on the attributions of the Palaeozoic species or, alternatively, reflects the extremely poor early Mesozoic freshwater fossil record. Additional species attributed to Lymnaeidae, Physidae, Pomatiopsidae, and Thiaridae in open nomenclature have been reported from Upper Triassic deposits of India (Nath, 1999). Yet, the taxonomy is highly doubtful again; for the purpose of this revision, these latter species are not considered herein as true first occurrences.

(b) Jurassic

Species diversity remained low during the Jurassic, but several new groups evolved (Figs 2 and 4). The Early Jurassic saw the (putative) first occurrences of Lymnaeidae (USA),

Carboniferous



Permian

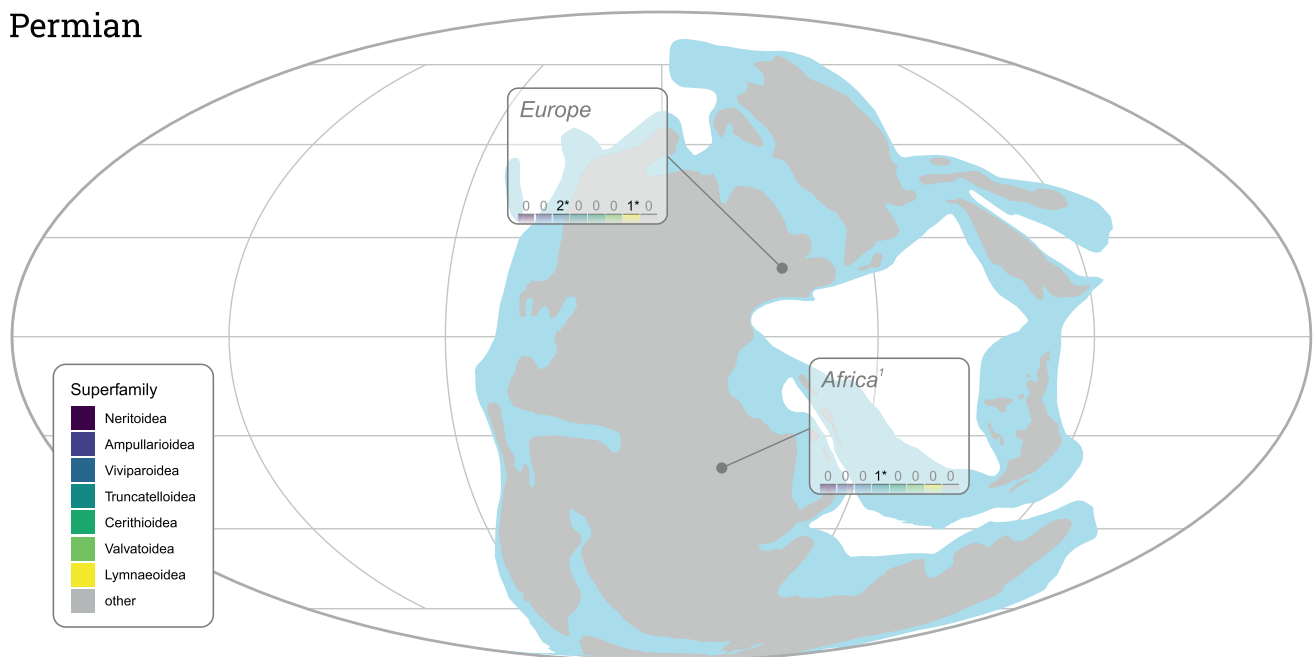
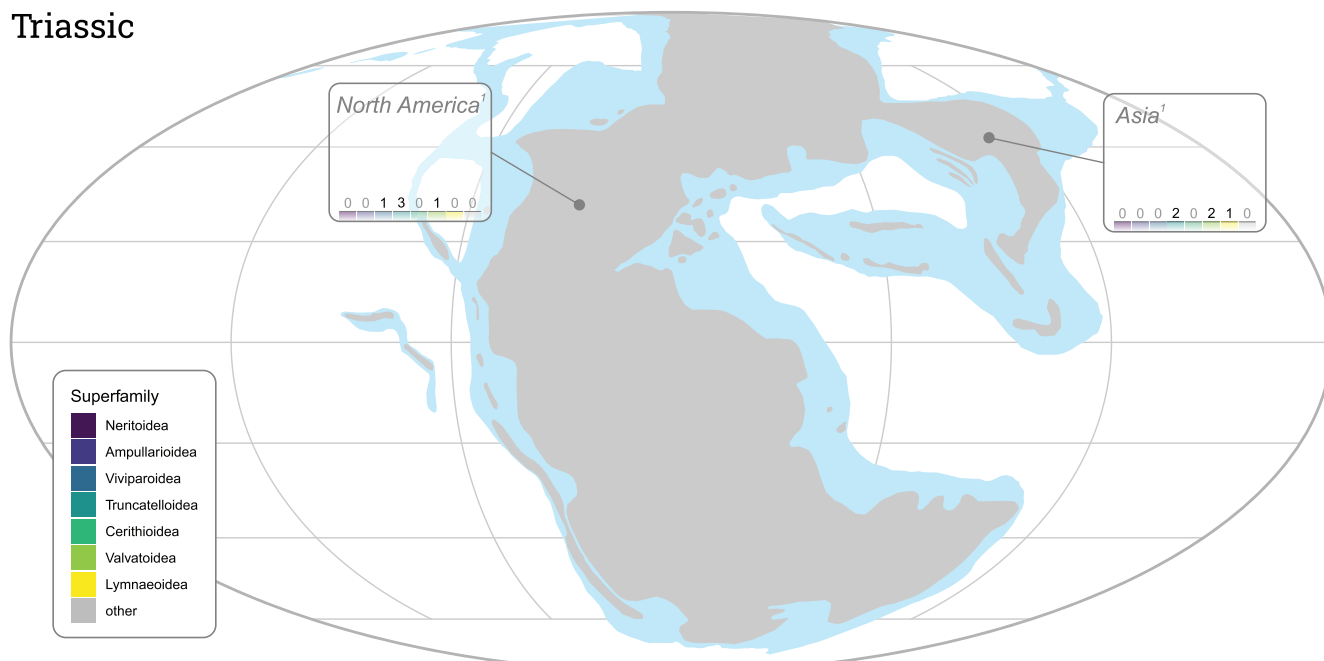


Fig. 3. Late Palaeozoic species diversity of freshwater/oligohaline gastropods per continent. Inserts indicate the numbers of species per superfamily. For Figs 3–6, diversity data are scaled to the maximum record (Neogene of Europe; see Fig. 6). Only taxa identified to species level are considered. Asterisks indicate records that include *taxa inquirenda*, some of which may constitute potential first occurrences of higher clades (Table S4). Superscript 1 after a continent name signifies the first freshwater/oligohaline fossil record for that continent. Continent delimitation is based on the present-day situation. Palaeogeographic reconstructions were modified from Kocsis & Scotese (2021) and show the continental configurations for the late early Carboniferous (Serpukhovian, 325 Myr ago) and early Permian (Kungurian, 275 Myr ago). Land masses are in grey, continental margins (–1400 m) in blue. Projection: Mollweide.

Bithyniidae (China), Neritidae (China), and Pachychilidae (Germany, China) (Pan, 1977, 1982; Salvador & Yu, 2022; Neubauer, 2023) (Fig. S2, Table S4). Pomatiopsidae followed during the Middle Jurassic in Yunnan (Pan, 1977; but see discussion on potential Indian Triassic

representatives in Section III.2.a) (Fig. S2, Table S4). The fossil family Provalvatidae (Valvatoidea), the Physidae, and the Hemisinidae first appeared during the Late Jurassic (Huckriede, 1967; Bandel, 1991) (Fig. S2, Table S4). Jurassic species diversity is highest in Asia, followed by Europe and

Triassic



Jurassic

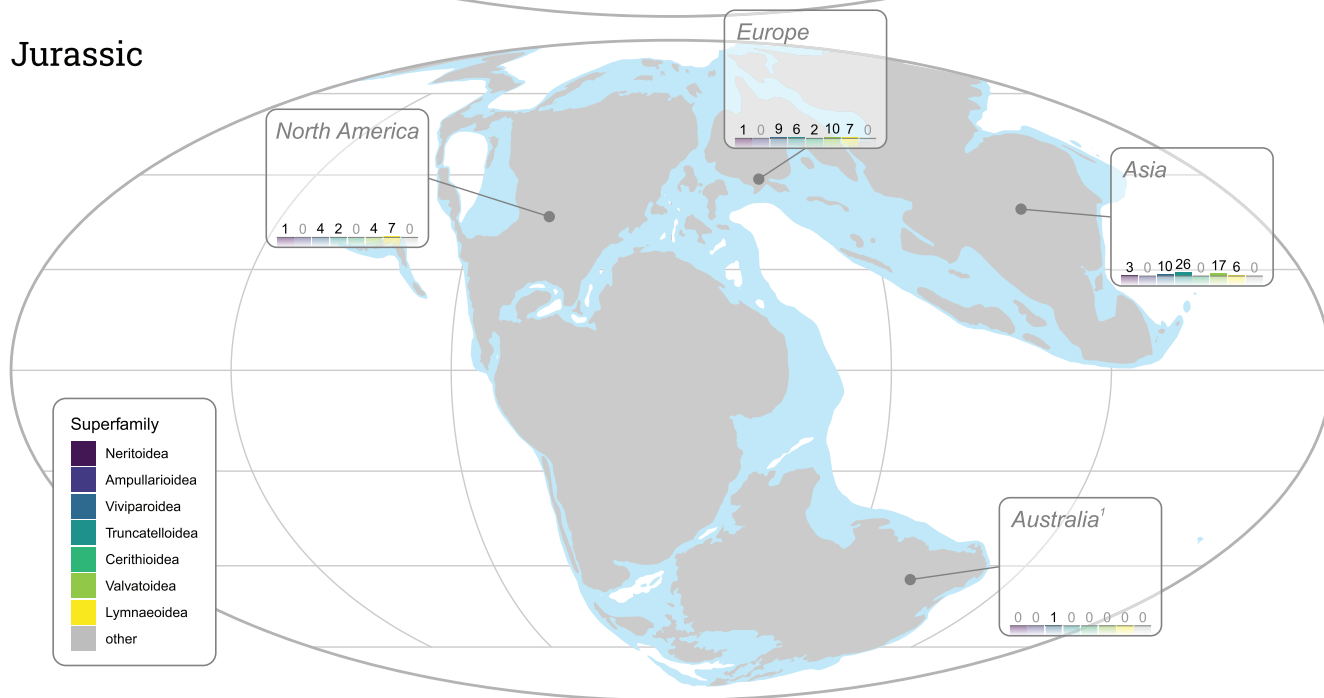


Fig. 4. Triassic and Jurassic species diversity of freshwater gastropods per continent. Map data as for Fig. 3, showing the palaeogeographic reconstructions for the Late Triassic (Norian, 220 Myr ago) and the Middle Jurassic (Bajocian, 170 Myr ago).

North America; only a single species has been described from the southern hemisphere: the viviparid *Proviviparus talbragarensis* Frese & Ponder, 2021 from Australia (Frese & Ponder, 2021). Notable for their diversity are the Middle Jurassic faunas of Yunnan (China; Pan, 1977) and the Late Jurassic faunas of Lower Saxony (Germany; Huckriede, 1967) and the Morrison Formation in western North America (Branson, 1964; Evanoff, Good & Hanley, 1998; Yen, 1952b). The latter coincides with the

formation of extensive wetlands following the retreat of a marine embayment that resulted in a first peak of freshwater gastropod species diversification in North America (Neubauer *et al.*, 2022a).

(c) Cretaceous

The number of species rose considerably over the Early Cretaceous, with the first appearance of numerous families:

Acroloxidae, Ampullariidae, Bulinidae, Cochliopidae, Lithoglyphidae, Melanopsidae, Pleuroceridae (?), Semisulcospiridae, Thiaridae, and the fossil-only families Mesocochliopidae, Palaeobaicaliidae, and Pliopholygidae (Russell, 1932; Delpey, 1940; Yen, 1951b; Martinson, 1957, 1982; Yü & Pan, 1980; Guo *et al.*, 1982; Yu, 1987; Bandel, 1991) (Figs 2, 5, S1 and S2, Table S4). As for the Triassic first occurrences discussed in Section III.2.a, Pleuroceridae have been hypothesised to have Palaeozoic roots (Yen, 1949a). However, the stratigraphic gap involves more than 150 Myr, questioning the classification of the Palaeozoic species into that family. For lithoglyphids, a Jurassic origin was hypothesised based on molecular dating by Hausdorf, Röpstorf & Riedel (2003), but this suggestion has been disputed (Wilke, 2004). Also based on molecular clock dates, Neiber & Glaubrecht (2019b) suggested younger ages for Pleuroceridae (Late Cretaceous) and Semisulcospiridae (Eocene).

Rich faunas are known from Europe (Huckriede, 1967; Bandel, 1991), North America (Russell, 1932; Henderson, 1935; Yen, 1949b), and Asia (Martinson, 1961; Yu, 1987) (Fig. 5). The stratigraphically oldest records for South America (Parodiz, 1969; Salvador *et al.*, 2018) are of Early Cretaceous age. The superfamilies Viviparoidea, Truncatelloidea, and Lymnaeoidea all diversified during the Early Cretaceous (Fig. S1). Cerithioids, by contrast, diversified particularly during the Late Cretaceous, with the first occurrences of Paludomidae (Sandberger, 1870–1875) in the Cenomanian and the truncatelloid family Tateidae (Parodiz, 1969) in the Maastrichtian (Fig. S2, Table S4). Given that the next oldest occurrence of the Tateidae is in the Middle Miocene

(Morton, 1986; Morton & Herbst, 2003) the supposed latest Cretaceous origin is possibly questionable.

Despite fewer first occurrences at the family level or above, the Late Cretaceous was a period of species- and genus-level diversification (Fig. 2). Diverse faunas are known from North America (Yen, 1952a, 1954; Tozer, 1956; Perrilliat *et al.*, 2008) and Asia (Martinson, 1961; Yü, 1977; Yü, Pan & Wang, 1982), and a peak in diversification noted for Europe (Mertin, 1939; Fabre-Taxy, 1951; Bandel & Riedel, 1994), likely related to global sea-level rise and the formation of extensive brackish-water habitats (Neubauer & Harzhauser, 2022).

(3) Unprecedented peaks of diversity: the Cenozoic

(a) Palaeogene

Despite a major species turnover at the Cretaceous–Palaeogene (K–Pg) boundary (Neubauer *et al.*, 2021), little changed in the Paleocene in terms of overall diversity (Fig. 2). Non-marine Irvadiidae (genus *Stenothyrella*; Kadolsky, 2022) and Truncatellidae (genus *Nystia*; Yü, 1977), as well as Bythinellidae (Cossmann, 1924; Glibert, 1973) and Stenothyridae (Yü, 1977) all appeared (Fig. S2, Table S4). A notable post-extinction fauna (of uncertain age) is documented from the border triangle constituted by Slovenia, Italy, and Croatia, i.e. the Liburnian freshwater fauna, which shows tremendous morphological and taxonomic diversity and a high degree of endemism (Stache, 1889). Rich Paleocene faunas have also been reported from the upper Willow Creek Formation (Tozer, 1956), the Ravenscrag Formation (Russell, 1974),

Cretaceous

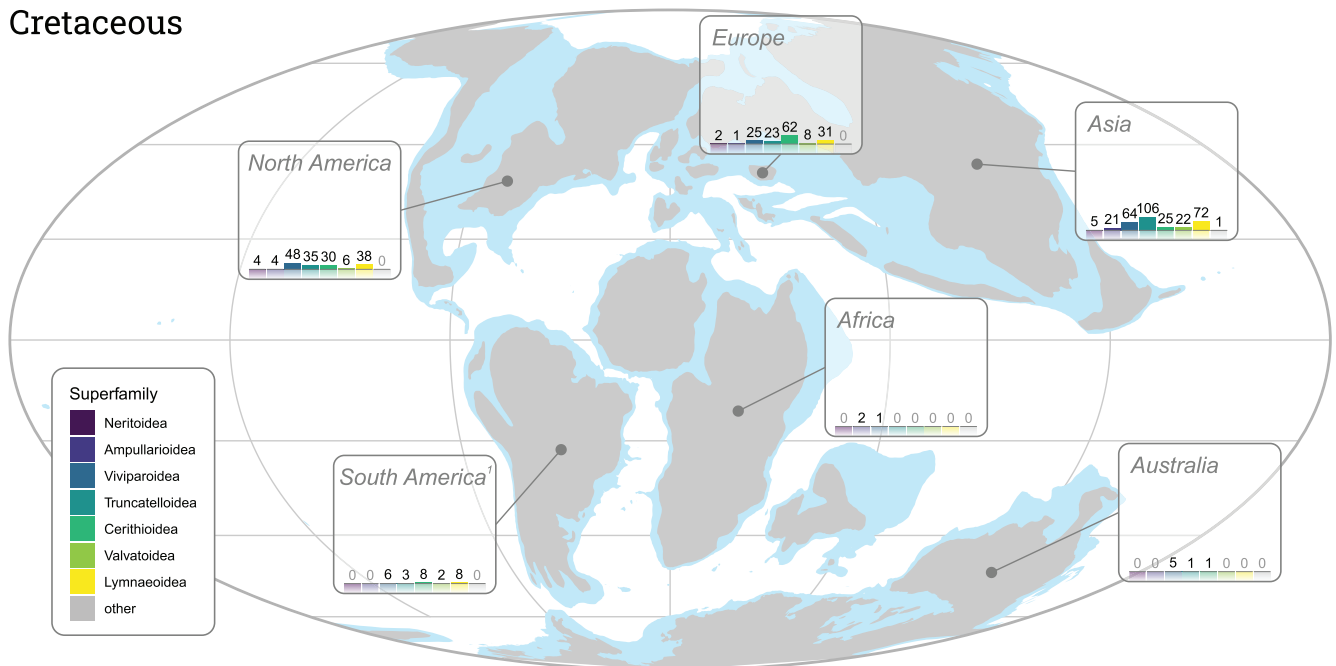


Fig. 5. Cretaceous species diversity of freshwater gastropods per continent. Map data as for Fig. 3, showing the palaeogeographic reconstructions for the Late Cretaceous (Cenomanian, 95 Myr ago).

the Paskapoo Formation (Russell, 1926; Tozer, 1956), the Green River Formation (Flagstaff Member; La Rocque, 1960), and the Fort Union Formation (Yen, 1948; Bickel, 1977; Hanley & Flores, 1987) in North America. A brackish–freshwater fauna is also known from the early Paleocene of Mons in Belgium (Glibert, 1973; Kowalke, 2002). The first freshwater elements appear in the Paris Basin (Pacaud, 2011; Leroy *et al.*, 2014), representing the beginning of an extensive fossil record of non-marine faunas that extends to the Early Miocene.

The Eocene saw a rise in global diversity (Fig. 2), with extensive diversification among Cerithioidea, Truncatelloidea, and Lymnaeoidea (Fig. S1), as well as the first occurrences of Bohaispiridae (Huang, 1983), Chiliniidae (and the superfamily Chilinoidea; Parodiz, 1969), Emmericiidae (Pacaud, 2008), Moitessieriidae (Pacaud & Le Renard, 1995), and Neritiliidae (Symonds & Tracey, 2014) (Figs S1 and S2, Table S4). Important centres of diversity in Europe include the Paris Basin in France (Pacaud & Le Renard, 1995; Pacaud, 2008) and the London and Hampshire basins in England (Wenz, 1923–1930; Symonds, 2002; Munt, 2014). In North America, a diverse Eocene fauna was reported from the Kishenehn Basin in Montana and British Columbia (Pierce & Constenius, 2001, 2014). Numerous rich faunas have furthermore been documented from China, specifically from Anhui (Yü *et al.*, 1982), Hebei (Yü & Pan, 1982), and Shandong (Youluo, 1978).

In the Oligocene, the family Zemelanopsidae, endemic to Zealandia, appeared in the fossil record (Neiber & Glaubrecht, 2019b) (Fig. S2, Table S4). In addition to the Paris Basin, noteworthy faunas are known from the Mainz Basin and Upper Rhine Graben in Germany (Wenz, 1923–1930; Gillet, 1953; Kadolsky, 1995), the widespread Upper Oligocene Formation du Gypse d'Aix (formerly known as 'ramondi beds') in the Alpine Foreland Basin (Wenz, 1923–1930), and the Cabbage Patch beds in Montana (Pierce, 1993). In China, several rich Oligocene assemblages have been documented from Hebei, Liaoning, Shandong, and Tianjin (Youluo, 1978), as well as the morphologically peculiar fauna of the Nanning Basin in Guangxi, featuring huge viviparids with extraordinarily thickened and armoured shells (Odhner, 1930; Ying, Fürsich & Schneider, 2013; Ying, Shaw & Schneider, 2018).

Across the entire Palaeogene, diversification was centred in Europe and Asia and to a lesser extent in North America (Fig. 6). African Ampullarioidea constitute a notable exception – compared to an otherwise poor African fossil record, this group diversified considerably during the Palaeogene (Mayer-Eymar, 1901; Jodot, 1953; Harzhauser *et al.*, 2017; Epa *et al.*, 2018).

(b) Neogene

The Miocene hosted the highest diversity among freshwater and oligohaline gastropods ever recorded (Fig. 2). The European fossil record alone includes 1969 species, accounting for 38.0% of all fossil species ever described globally

(Fig. 6). A large part of that diversity is centred on long-lived lakes, such as Lake Pannon in the Late Miocene of central to south-eastern Europe (Harzhauser & Mandic, 2008; Magyar *et al.*, 2013; Neubauer *et al.*, 2016c) or the numerous lakes of the Early–Middle Miocene Dinaride Lake System on the Balkan Peninsula (Mandic *et al.*, 2009; Mandic, Harzhauser & Neubauer, 2020; De Leeuw *et al.*, 2011; Harzhauser *et al.*, 2012; Neubauer, Mandic & Harzhauser, 2016d; Neubauer *et al.*, 2020). A more detailed assessment of the importance of long-lived lakes in species diversification is provided in Section VI.

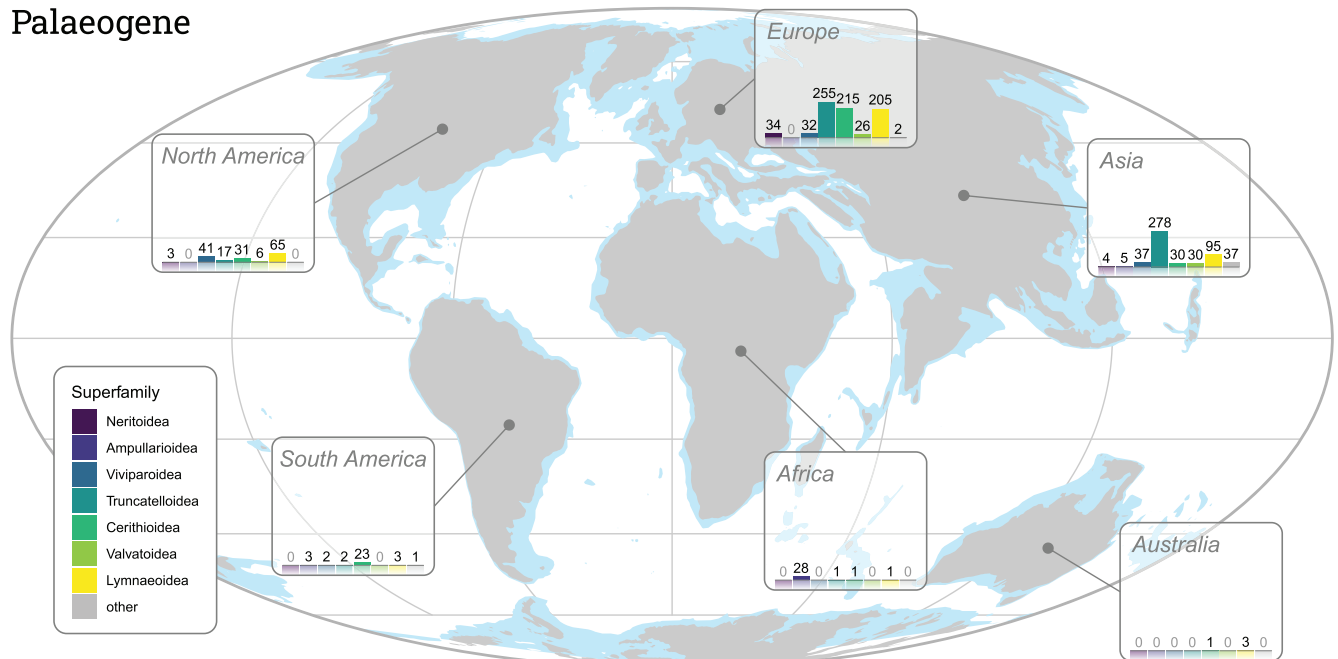
In contrast to Europe, species diversity in North America remained more similar to that during the Palaeogene, while it decreased in Asia (Fig. 6). South American diversity rose considerably, especially among Truncatelloidea. This peak can be almost exclusively attributed to diversification in a single ecosystem, the Miocene Pebas wetland (Nuttall, 1990; Wesselingh, 2006a,b). The African fossil record showed a similarly increased number of species, concentrated primarily in the northwest (Morocco and Algeria; Bourguignat, 1862; Pallary, 1901) and central Africa (Uganda, Democratic Republic of the Congo; Gautier, 1970; Gautier & Van Damme, 1973; Van Damme & Pickford, 1995, 1999, 2003; Musalizi, 2017). By contrast, only three species are known from the Miocene of Australia (McMichael, 1968; Marshall, 2011). Amphimelaniidae (Wenz, 1923–1930), Latiidae (Marshall, 2011), the fossil-only Clivunellidae, a family of limpet-like Lymnaeoidea (Kochansky-Devidé & Slišković, 1972; Harzhauser & Mandic, 2008), and aquatic Succineidae (genus *Papyrotheca*; Lörentz, 1895) first appeared during the Miocene (Fig. S2, Table S4).

The Pliocene saw several centres of diversification for freshwater gastropods in Europe. Most prominent are the Dacian Basin in southern Romania, Lake Slavonia spanning north-eastern Croatia, western Serbia, and southern Hungary, as well as Lake Transylvania in the Braşov Basin in Romania (Jekelius, 1932; Jipa & Olariu, 2009; Andreescu *et al.*, 2013; Mandic *et al.*, 2015; Lazarev *et al.*, 2020) including several hundreds of species and high degrees of endemism (Neubauer *et al.*, 2015b,c, 2016c). The family Viviparidae particularly experienced numerous independent diversification events across different regions (e.g. Lubenescu & Zazuleac, 1985; Mandic *et al.*, 2015) (Fig. S2). Pliocene centres of diversity in Asia are found in Turkey (Oppenheim, 1919; Taner, 1997) and Siberia (Popova, Devyatkin & Starobogatov, 1970). The oldest Fontigentidae are found in the Late Pliocene of Florida (Pilsbry, 1953) (Fig. S2, Table S4).

(c) Quaternary

The Pleistocene fossil record is a potpourri of species that are still living today (which are not considered herein), those in fading large Plio–Pleistocene freshwater systems, and a lower number of taxa that are stratigraphically confined to the Pleistocene. The majority of Pleistocene species diversity again derives from Europe. Most of the diverse freshwater

Palaeogene



Neogene

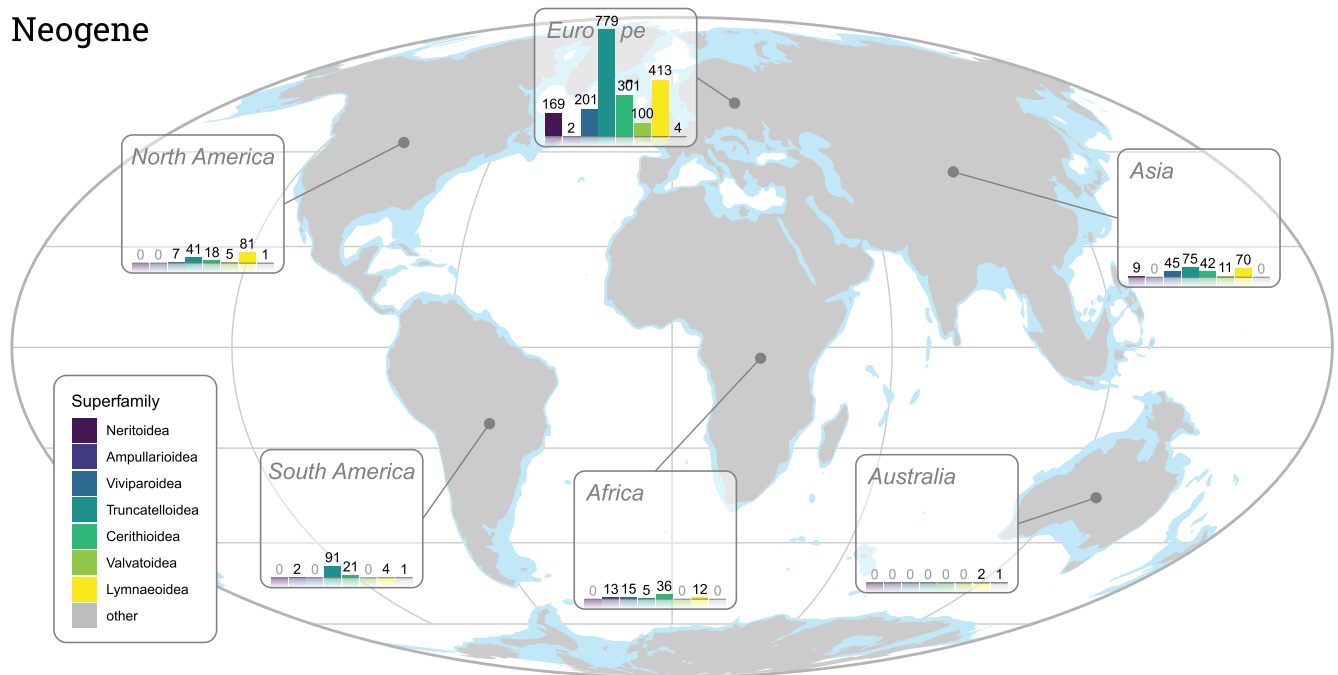


Fig. 6. Palaeogene and Neogene species diversity of freshwater gastropods per continent. Map data as for Fig. 3, showing the palaeogeographic reconstructions for the Eocene (Lutetian, 45 Myr ago) and the Miocene (Langhian, 15 Myr ago) respectively.

systems of the Pliocene, such as Lake Slavonia, Lake Dacia, and the fluvio-lacustrine systems in the Bresse Basin and the Aegean islands Kos and Rhodes, extend into the earliest Pleistocene (Willmann, 1981; Jipa & Olariu, 2009; Mandic *et al.*, 2015; Neubauer *et al.*, 2015b). Additionally, diverse freshwater faunas have been reported from the Pontocaspian region (Kolesnikov, 1950; Ali-Zade, 1969, 1973; Neubauer *et al.*, 2018; van de Velde *et al.*, 2020), Italy

(Esu & Girotti, 1975, 2020; Petronio *et al.*, 2003), and Spain (Jodot, 1958; Madurga, 1973; Anadón, De Deckker & Julià, 1987; Robles, 1989). The available Asian fossil record is concentrated in western Asian countries (Turkey, eastern Caspian region and Near East; Ali-Zade, 1967; Rausch *et al.*, 2019; T.A. Neubauer & F.P. Wesselingh, unpublished data). Additional records come from China, Russia, India, Myanmar, and Indonesia (Annandale, 1919; Prashad, 1930;

van Benthem Jutting, 1937; Popova, 1968; Li, 1988). North American Pleistocene faunas are very common and well studied (e.g. Russell, 1934; Leonard, 1957; Taylor, 1965; La Rocque, 1968), but no exceptionally diverse or endemic fauna is known. A few Pleistocene-only species are known from Africa, specifically from north-western Africa (Paladilhe, 1874; Pallary, 1901) and the African Rift Valley region (Charig, 1970; Van Damme & Pickford, 2003). None are recorded from South America, and only two from Australia, which at the same time represent the first appearances of the families Glacidorbidae (and thus the superfamily Glacidorboidea; Ponder & Avern, 2000) and Tomichiidae (Kendrick, 1978) in the fossil record (Figs S1 and S2, Table S4).

No fossil-only species are known for: (i) Acochlidimorpha, comprising 12 living freshwater species in the families Tantulidae and Acochliidae [although a Jurassic origin was suggested by Jörger *et al.* (2010, 2014) based on molecular clock dates]; (ii) the lymnaeoid family Burnupiidae, containing 22 extant species of the single genus *Burnupia* (molecular data indicate a Miocene age for the group; Sands *et al.*, 2022); (iii) the truncatelloid family Clenchellidae, consisting today of four genera and 14 species (MolluscaBase eds, 2023). Until recently, the Helicostoidae would have been included in that list, containing the single enigmatic sessile (and probably recently extinct) species *Helicostoa sinensis*. Recent molecular analyses however found this species to be related to Bithyniidae and classified it in the subfamily Helicostoinae (Wilke *et al.*, 2023).

IV. COLONISATION OF FRESH WATER

Gastropods conquered freshwater habitats multiple times independently throughout Earth's history. Transitions happened in three out of the six extant subclasses of gastropods (Caenogastropoda, Heterobranchia, and Neritimorpha), but not in Vetigastropoda, Neomphaliones, and Patellogastropoda (Fig. 7). Most freshwater lineages descend from Caenogastropoda, compared to 5–6 each in Heterobranchia and Neritimorpha. Only considering extant species, the latest estimates indicate around 32–37 independent freshwater lineages distributed across multiple major clades (Strong *et al.*, 2008; excluding the now redundant Helicostoidae, see Section III.3.c). The highest number of colonisation events is recorded for Truncatelloidea [part of the 'rissoiform clade' *sensu* Bouchet *et al.* (2017)], specifically for families Assimineidae (at least 2), Cochliopidae (at least 2), Pomatiopsidae (1–2), Stenothyridae (at least 1), Lithoglyphidae (at least 1), Moitesseriidae (at least 1), Bithyniidae (1), and Hydrobiidae (6–8?). Cerithioidea include 2–3 transitions to fresh water, Architaenioglossa probably 2, Littorinidae 1, Buccinidae 1, Marginellidae 1, Neritimorpha 5–6, Acochlidimorpha probably 2, Glacidorbidae 1, Valvatidae 1, and Hygrophila 1 (Strong *et al.*, 2008; Fig. 7). Some of these invasions reflect the transition of only a single genus (Miller & Labandeira, 2002; Strong *et al.*, 2008; Jörger *et al.*, 2010).

Including the fossil record, the total number of colonisation events is probably much higher, but the exact number is difficult to assess, partly because of unresolved systematic relationships (Strong *et al.*, 2008), and partly because the type of environment (e.g. brackish *versus* freshwater) cannot always be unambiguously determined in the sedimentary record. Moreover, shells retrieved from freshwater strata do not necessarily belong to species that lived in freshwater conditions but may have been transported from elsewhere, as is frequently the case for terrestrial snails (e.g. Harzhauser *et al.*, 2014; Hölte & Rasser, 2017).

Following current systematic attributions, additional probable colonisations of freshwater environments are indicated for species of Ellobiida in the Early Cretaceous of Japan (Isaji, 2010) and the Late Jurassic–Early Cretaceous of Europe (Purbeck beds; Dayrat *et al.*, 2011). Moreover, several fossil-only families exist in higher clades that contain both marine and freshwater taxa, such as Bohaispiridae (Littorinoidea), Mesocochliopidae, Palaeobaicaliidae (both Truncatelloidea), and Provalvatidae (Valvatoidea). It is unknown whether they represent distinct colonisation events or branches of other clades that entered freshwater ecosystems earlier.

Yen (1952b) introduced the new genus *Limnopsis* for a Jurassic freshwater taxon and classified it in Otinidae, an otherwise marine, coastal group. Because of differences in shell morphology, the otherwise virtually absent fossil record of Otinidae and the ecological discrepancy, Dayrat *et al.* (2011) doubted that assignment; a taxonomic revision is still pending.

The fossil record probably saw numerous independent transitions within single families, especially among those with broader ecological ranges. A prime candidate is the family Melanopsidae, which derives from brackish-water ancestors in the Cretaceous and since then has diversified taxonomically, morphologically, and ecologically (Glaubrecht, 1996; Bandel, 2000; Geary *et al.*, 2012; Neubauer *et al.*, 2013, 2016b; Neubauer, 2016). While melanopsids were mainly restricted to marginally marine to brackish-water environments during the Cretaceous and Palaeogene, Neogene representatives probably invaded freshwater ecosystems in several independent events. Putative transitions to fresh water include the colonisation of the Early–Middle Miocene Dinaride Lake System in Croatia and Bosnia and Herzegovina, the Pliocene Lake Slavonia, which derived from brackish Lake Pannon, or the Late Miocene–Early Pleistocene Dacian Basin fauna, which experienced a transition from brackish to fresh water in the Pliocene (Jipa & Olariu, 2009; Mandić *et al.*, 2015; Neubauer *et al.*, 2016c). Especially from the Pliocene onwards, melanopsid species are mainly found in freshwater ecosystems (Glaubrecht, 1996; Neubauer *et al.*, 2016b; Neiber & Glaubrecht, 2019b).

The same may be true for Hydrobiidae, which are also found in the abovementioned faunas. Considering their obvious affinity to freshwater colonisation as evident from extant

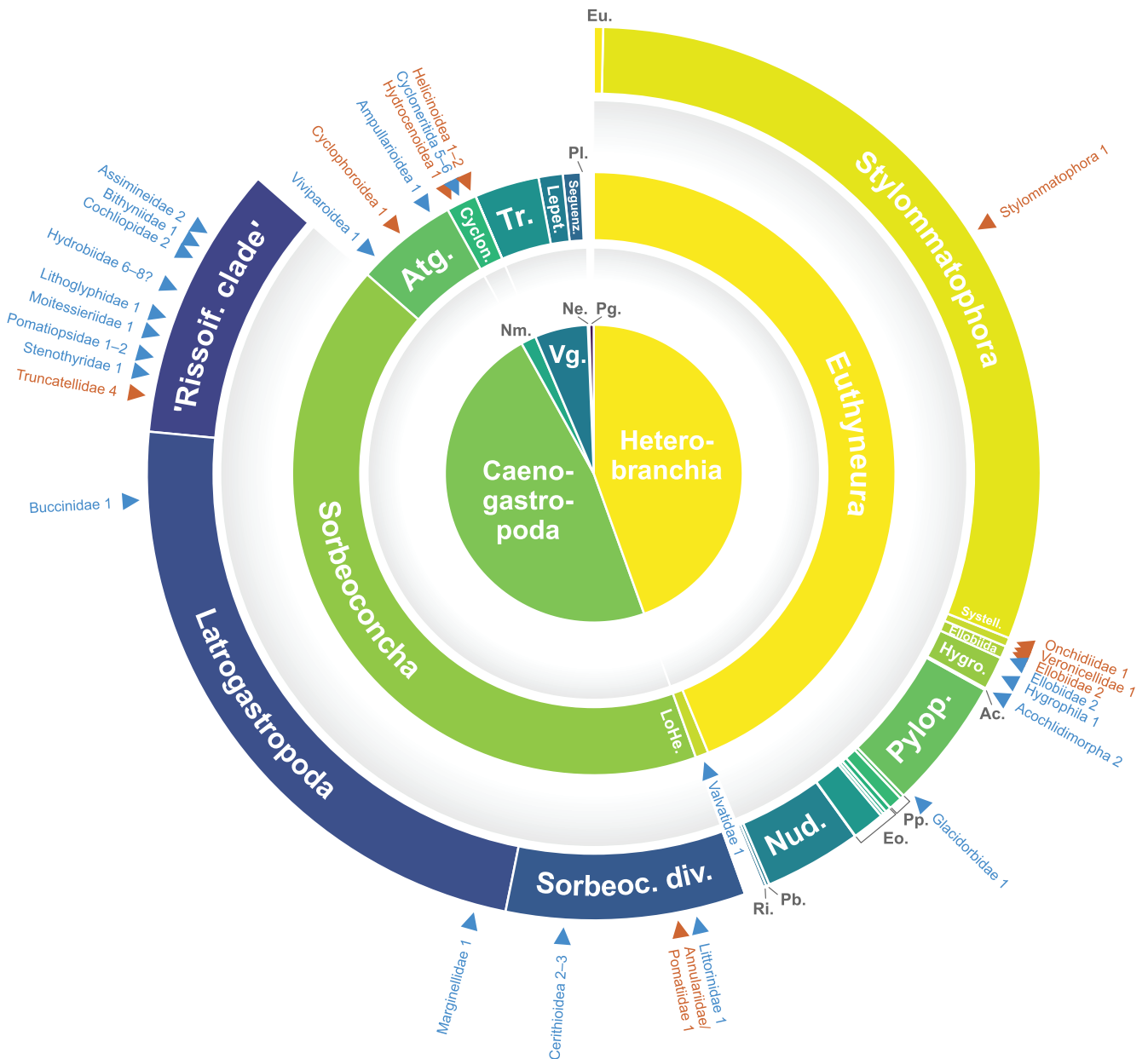


Fig. 7. Non-marine colonisation events among Gastropoda. Transitions to fresh water are indicated in blue, those to land in red; marine–brackish transitions are not considered here. Number of colonisations follows Vermeij & Dudley (2000), Kano *et al.* (2002), Strong *et al.* (2008), and Dayrat *et al.* (2011), with updates based on this review. Relative diversity of higher clades according to MolluscaBase (extant species only); systematics following Bouchet *et al.* (2017). Ac., Acochlidimorpha; Atg., Architaenioglossa; Cyclon., Cycloneritida; Eo., Euopisthobranchia; Eu., other Euthyneura (taxa of uncertain position); Hygro., Hygrophila; Lepet., Lepetellida; LoHe., ‘Lower Heterobranchia’; Ne., Neomphaliones; Nm., Neritimorpha; Nud., Nudibranchia; Pb., Pleurobranchia; Pg., Patellogastropoda; Pl., Pleurotomariida; Pp., other Panpulmonata (Sacoglossa, Siphonarimorpha); Pylop., Pylopulmonata; Ri., Ringiculida; Rissoif., rissoiform; Seguenz., Seguenziida; Sorbeoc. div., remaining Sorbeoconcha; Systell., Systellommatophora; Tr., Trochida; Vg., Vetigastropoda.

lineages (Strong *et al.*, 2008), it is likely that there were several (if not numerous) independent transitions to fresh water in that family in the geological past.

Figure 7 includes only transitions to fresh water. Examples of notable brackish clades that may have marine ancestors include one (or a few) genera in Truncatellidae

(Kadolsky, 1993; Kadolsky & Morton, 2022) and Iravadiidae (Lozouet, 2003; Kadolsky, 2022).

Current knowledge suggests that all mollusc colonisations of freshwater habitats took place from the marine realm. Two pathways are conceivable: colonisation may take place either *via* deltas with brackish embayments or lagoons, where

a river discharges behind a barrier and thus creates a gradual transition from marine to freshwater conditions, or more directly *via* estuaries, where the transition occurs within the tidally influenced part of the river. One exception to the pattern of marine-derived colonisations is the enigmatic genus *Papyrotheca*, which may have originated from a terrestrial Succineidae (Stylommatophora) ancestor in the Late Miocene brackish Lake Pannon, although this taxon is not known from true freshwater ecosystems (Vermeij & Dudley, 2000; Harzhauser & Mandic, 2008; Harzhauser & Neubauer, 2021). Earlier works hypothesised a transition from terrestrial to fresh water for the superorder Hygrophila (pulmonate gastropods; Miller & Labandeira, 2002), but ancestral state reconstructions suggest a single marine to freshwater transition at the base of Hygrophila (Klussmann-Kolb *et al.*, 2008).

V. GASTROPODS ON LAND

Gastropods have played an important role in freshwater ecosystems in Earth history, especially in the late Mesozoic and Cenozoic. However, today freshwater gastropods, at 5260 species, account for only 15.6% of non-marine gastropod diversity, compared to the extraordinarily high diversity of ~28,400 species (84.4%) of terrestrial snails (MolluscaBase eds, 2023). The fossil record of land snails is rather poor and includes only 2280 species in total (i.e. less than half the number of fossil freshwater gastropod species; MolluscaBase eds, 2023).

Gastropods on land have a similarly long fossil record as freshwater gastropods. The oldest fossils of land snails date back to the late Carboniferous (Solem & Yochelson, 1979). Earlier records are all systematically or stratigraphically doubtful or have been proved incorrect (Solem & Yochelson, 1979). The late Palaeozoic inventory of land snails contains 11 species (13 when including *taxa inquirenda*), and thus is as sparse as that for freshwater gastropods. Following current systematics, these early representatives probably all belong to Stylommatophora (Jochum, Yu & Neubauer, 2020).

No Triassic land snails are known, and for the Jurassic there are only patchy records of Stylommatophora as well as the first Cyclophoroidea (Bandel, 1991; Jochum *et al.*, 2020). Species diversification accelerated especially in the Late Cretaceous (Matheron, 1843; Oppenheim, 1895; Wenz, 1940; Hrubesch, 1965; Balashov, 2021; Bichain *et al.*, 2022). As for freshwater gastropods, diversity in the Cenozoic increased considerably towards the Miocene, but experienced a strong decline at the Pliocene–Pleistocene boundary (Harzhauser & Neubauer, 2021).

There were probably 13–14 independent colonisation events for land snails, which is much lower than for their freshwater counterparts (Fig. 7). In Caenogastropoda this includes 1 in Architaenioglossa (Cyclophoroidea) in the Late Jurassic, at least 1 in the sorbeoconch superfamily Littorinoidea (Annulariidae, Pomatiidae) in the Late Cretaceous

(Nicolas, 1898; Fabre-Taxy, 1959; Hrubesch, 1965), and at least 4 independent events in the truncatelloid family Truncatellidae (Vermeij & Dudley, 2000). Among Neritimorpha there was at least one event in Hydrocenoidea and 1–2 in Helicinoidea (Kano, Chiba & Kase, 2002). Marine–land transitions in Heterobranchia include at least 2 events in Ellobiida (Carychiinae and one genus of Pythiinae; not considering amphibious species), 2 in Systellommatophora (Veronicellidae and one genus in Onchidiidae) and probably a single event at the base of Stylommatophora (Dayrat *et al.*, 2011). That single basal event in Stylommatophora has led to the ~22,400 extant species of land snails (~79% of total terrestrial snail species diversity), making this particular transition probably the most successful colonisation event among Gastropoda.

The comparatively low diversity of terrestrial gastropods in Earth history and the low number of colonisation events known to date are to some extent the result of a major preservation bias. As stated above, fossil terrestrial snails are frequently retrieved from freshwater strata (e.g. Harzhauser *et al.*, 2014; Hölte & Rasser, 2017), which have a higher preservation potential than their autochthonous terrestrial habitat. One exception is formed by rich but rare amber deposits, such as Burmese amber (Balashov, 2021; Bichain *et al.*, 2022).

VI. THE UNEVEN DISTRIBUTION OF DIVERSITY

Species diversity is unevenly distributed across space and time. By far the largest number of fossil freshwater gastropod species – 3078, representing 59.4% of the global fossil record – have been described from Europe (Fig. 8). A large number of these were described from long-lived lakes, which were particularly widespread in the European Neogene (Harzhauser & Mandic, 2008; Neubauer *et al.*, 2015b,c, 2016c; Neubauer & Georgopoulou, 2021). Asia follows with 1268 species, reflecting the diverse Mesozoic and Cenozoic lake systems particularly in China, Siberia, and Mongolia (Martinson, 1961, 1982; Pan, 1977; Youluo, 1978; Kolesnikov, 1980), compared to a relatively poor record in tropical Asia. The North American fossil record yielded 507 species, mainly from the west to mid-west USA and southern Canada (Henderson, 1935; Neubauer *et al.*, 2022a). The continents of the southern hemisphere are comparatively poor in fossil freshwater gastropods (Fig. 8). One hundred seventy nine species are known from South America, mostly from the Neogene Pebas wetlands in Peru, Colombia, and NW Brazil (Wesselingh *et al.*, 2002; Wesselingh, 2006a,b), 140 from Africa, with a centre of diversity in the African rift valley (e.g. Gautier & Van Damme, 1973; Van Damme & Pickford, 1994; Musalizi, 2017), and only 17 from Australia and New Zealand. The only fossil freshwater gastropod recorded from Antarctica is an unidentified lymnaeid fragment from the (supposedly) Pliocene Meyer Desert Formation (Ashworth & Preece, 2003).

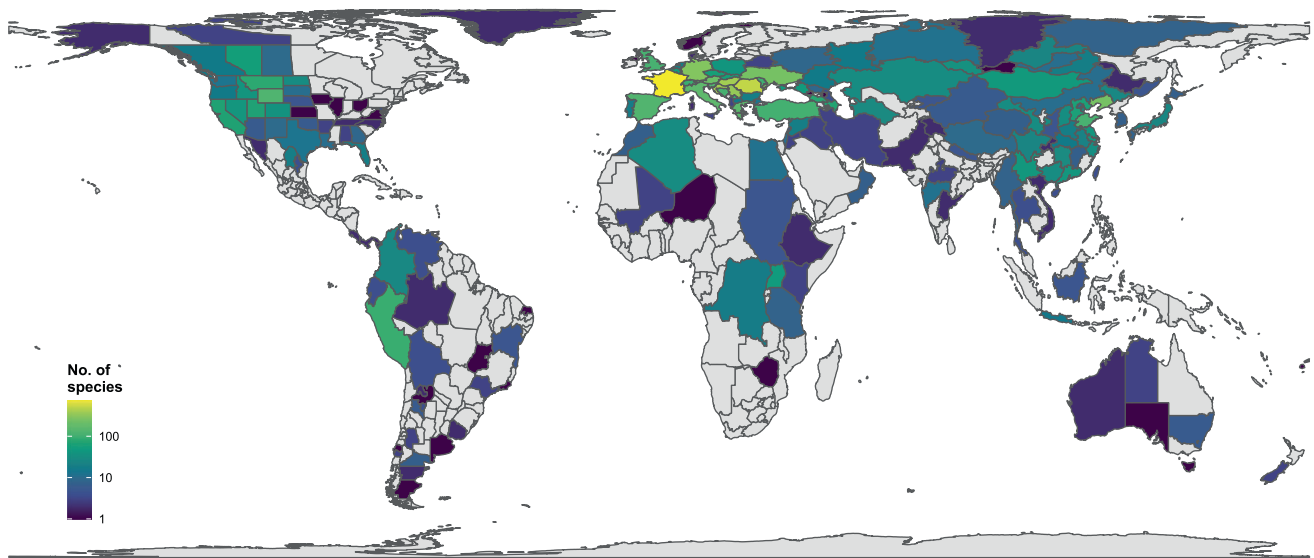


Fig. 8. Species diversity of the global fossil record of freshwater/oligohaline Gastropoda per Taxonomic Databases Working Group (TDWG) level-4 polygon, illustrating the uneven geographic distribution of diversity. Polygons largely match countries or, in the case of larger nations, higher administrative units or states (Brummitt, 2001). Species diversity was $\log_{10}$ -transformed to minimise the impact of exceptionally diverse regions (e.g. France). Islands smaller than 500 km² were omitted. Note that the apparent absence of a fossil record in certain polygons (grey) does not necessarily mean that there are no fossil freshwater gastropods in these regions but may reflect the incompleteness of the available distribution records (see Section VI) or records in open nomenclature. Some distributions are only available at a lower resolution (TDWG level-2/3 polygons). Projection: Behrmann.

The non-uniform distribution of freshwater gastropod diversity has various causes, including both drivers of diversification (see below) and biases due to preservation, sampling, and research focus and history. As a general rule, older sedimentary strata form a smaller portion of the rock record (Holland, 2016). In the case of freshwater molluscs, ecological restrictions to lakes, rivers or wetlands further constrains their possibility of preservation. Here, the available rock record is linked to the formation of intracratonic or epicontinental sedimentary basins and the associated freshwater deposits and their erosion, causing non-uniform preservation likelihood through space and time (Cohen, 2003; Holland, 2016). Lakes often have a long-term and rich sedimentary archive (e.g. Gierlowski-Kordesch & Kelts, 1994, 2000; Cohen, 2003; Mandic *et al.*, 2009). The preservational bias particularly favours lacustrine sediments in stable, tectonic basins (Cohen, 2003). Europe has accommodated numerous long-lived lakes in the geological past (Harzhauser & Mandic, 2008; Neubauer *et al.*, 2015b,c; Neubauer & Georgopoulou, 2021). Other continents harboured fewer of these sedimentary archives, e.g. the Pebas wetland (Wesselingh, 2006a, 2007), Lake T'oo'dichi' in North America (Turner & Fishman, 1991; Neubauer *et al.*, 2022a), Lake Nanning in China (Ying *et al.*, 2018), and Lake Turkana in eastern Africa (Wesselingh, 2007; Van Bocxlaer, Van Damme & Feibel, 2008). In contrast to lakes, rivers have a comparatively poor preservation potential due to their high hydrodynamic energy (Holland, 2016) resulting in the fragmentation, abrasion, disarticulation or

complete obliteration of freshwater mollusc shells (Nielsen, Helama & Nielsen, 2008). In addition, waters in many rivers and streams, as well as some ponds or lakes, are undersaturated in dissolved carbonate. As a result, carbonate is rapidly leached from shells after death, or earlier if the periostracum is damaged (Nielsen *et al.*, 2008; Araujo *et al.*, 2017). It is such streams that provide key hotspots for mollusc diversity today, with notable examples including the Lower Mekong River in South-east Asia, the Mobile River Basin in the southern USA, and the Congo in central Africa (Taylor, 1988; Strong *et al.*, 2008; Johnson *et al.*, 2013; Sor *et al.*, 2020). Moreover, as discussed in Section IV, rivers probably represented gateways for the colonisation of freshwater ecosystems.

A second factor is uneven research history across continents. Europe has the longest and most intense research history, with hundreds of publications dealing with fossil non-marine Mollusca (Wenz, 1923–1930; Harzhauser & Mandic, 2008; Neubauer *et al.*, 2015a,b,c; Neubauer, 2023). European naturalists started describing fossil freshwater gastropods in the 18th century (Brander, 1766). By the mid-19th century numerous species and faunas had been described, while in North America research on fossil freshwater gastropods was much slower to commence. Studies on other continents are largely restricted to the 20th and 21st century. This historical bias may explain to some extent the comparatively low recorded diversities in Africa, South America, Australia, and large parts of Asia. This bias may be enhanced by limited accessibility and patchy geological exploration across large parts of these continents.

Diversification is governed by a complex interaction of biotic and abiotic, extrinsic and intrinsic factors that act on different spatial, temporal, and ecological scales (e.g. Rabosky, 2013; Silvestro *et al.*, 2015; Ezard & Purvis, 2016; Jezkova & Wiens, 2017; Lehtonen *et al.*, 2017; Bush & Payne, 2021; Rabosky & Benson, 2021; Neubauer *et al.*, 2022b). The diversification history of freshwater gastropods is linked to tectonics, continental palaeogeography, and large-scale climatic developments, which control the availability and persistence of freshwater ecosystems across space and time (Neubauer *et al.*, 2015b,c, 2022a,b; Neubauer & Harzhauser, 2022).

Of particular relevance for the diversification history of freshwater gastropods is the formation of long-lived (ancient) lakes. In addition to their role as sedimentary archives, these ecosystems represent islands of evolution. Both in the fossil record and today, their extended temporal persistence has allowed freshwater biota to evolve extraordinary levels of taxonomic, phylogenetic, and phenotypic diversity (Michel, 1994; Martens, 1997; von Rintelen, Bouchet & Glaubrecht, 2007; Wesselingh, 2007; Albrecht & Wilke, 2008; Harzhauser & Mandic, 2008; Neubauer *et al.*, 2015b,c, 2016c; Hampton *et al.*, 2018; Neubauer & Georgopoulou, 2021). Long-lived lakes form the foundation for intralacustrine adaptive radiations, shown by numerous examples across continents, stratigraphic intervals, and taxa (Michel, 1994; Schön & Martens, 2004; von Rintelen *et al.*, 2004; Neubauer *et al.*, 2013; Salzburger, Van Bocxlaer & Cohen, 2014; Van Bocxlaer *et al.*, 2020). These cradles of evolution have delivered the majority of all known fossil freshwater gastropods globally. For example, 579 species have been recorded from a single system, Lake Pannon (Neubauer *et al.*, 2016c), accounting for 11.2% of all fossil freshwater gastropod species. Apart from the sometimes astounding levels of species diversity, the most extraordinary cases of shape and size evolution in freshwater gastropods derive from long-lived lakes. Notable examples include: (i) the huge, limpet-shaped lymnaeids of the subfamily Valencienniinae, which evolved in the Late Miocene in Lake Pannon from small ancestors of the genus *Radix* (Gorjanović-Kramberger, 1923; Taktakishvili, 1967; Neubauer *et al.*, 2016a; Neubauer, 2023); (ii) the Middle Miocene *Gyraulus* species flock in the Steinheim Basin (Hilgendorf, 1867; Mensink, 1984; Rasser, 2013); (iii) the Plio–Pleistocene *Viviparus* species flock in Lake Slavonia (Neumayr & Paul, 1875); (iv) the middle Miocene to Pliocene ‘*Kosovia*’–*Popovicia* lineage (Bulinidae) in Serbia and Kosovo, showing the step-wise evolution of sculptured sinistral *Bulinus* to pseudodextral, planorbiform morphologies (Atanacković, 1959; Popović, 1964; Milošević, 1970; Neubauer *et al.*, 2017); and (v) the cochliopid radiation in the Miocene Pebas wetland in South America (Wesselingh, 2006a,b; Wesselingh & Renema, 2009).

The non-uniform spatial distribution of freshwater gastropod diversity, paired with the underlying causes of ecosystem formation and demise as a result of interacting geodynamic and climatic processes, shows the importance of one overarching driver: ecological opportunity. This

term is typically used in the context of adaptive radiation and commonly relates to niche and resource availability as a basis for diversification (Schluter, 2000; Wellborn & Langerhans, 2015; Wilke *et al.*, 2020). In this context, the concept usually refers to a single clade or ecosystem. In a deep-time, global context, it can be expanded towards general habitat availability (and stability) as the required prerequisite for diversification on large spatial and temporal scales. To avoid confusion with the original use of ecological opportunity, I propose a new, slightly altered term: scale-independent ecological opportunity. This combines all abiotic and biotic conditions that lead to the ecological requirements facilitating diversification of a given clade. In the case of freshwater gastropods, this may involve the formation of stable, long-lived freshwater ecosystems.

Scale-independent ecological opportunity is not limited to freshwater clades, but can be applied to any animal and plant taxon and across continents and geological time intervals. However, given the isolated nature of freshwater habitats and lakes in particular, scale-independent ecological opportunity may have a more profound impact on diversification patterns in freshwater organisms, at least across large spatio-temporal scales. Comparable patterns may be expected for similarly isolated ecosystems, such as islands (Whittaker & Fernández-Palacios, 2007; Losos & Ricklefs, 2009) or mountain tops (Hoorn *et al.*, 2013; Zizka & Antonelli, 2018).

VII. CONCLUSIONS

- (1) The global fossil record of freshwater/oligohaline Gastropoda includes 5182 species in 490 genera, 44 families, and 12 superfamilies and spans ~340 million years (Carboniferous–Pleistocene). The most abundant group is the superfamily Truncatelloidea with 1906 species (with the family Hydrobiidae comprising 1102 species), followed by Lymnaeoidea (1142 species), Cerithioidea (900 species), Viviparoidea (600 species), and Neritoidea (241 species).
- (2) The earliest fossil record in the late Palaeozoic is patchy at best and consists of only a few species. A slightly more diversified and wider distributed record is found for the Triassic and Jurassic, but, as for Palaeozoic taxa, many of the systematic attributions are doubtful. This especially concerns the putative first occurrences of higher clades. This review summarises those early questionable cases, which will need to be studied further to improve our understanding of freshwater gastropod evolution. Several clades originated in the Early Cretaceous, leading to increased diversity. An all-time species diversity peak is reached in the Neogene, coinciding with the development of numerous long-lived lakes and biodiversity hotspots at that time.
- (3) Colonisation of freshwater ecosystems from marine ancestors occurred multiple times independently in the geological past. Summarising all known and putative transitions to fresh water, at least 32 independent colonisation events

across 20 clades are known. Considering the uncertain systematic classifications of some of the fossil families as well as the more euryoecious groups (such as Melanopsidae and Hydrobiidae), the actual number is probably higher. However, the current estimate exceeds the 13–14 transitions (in 9 clades) to land. While terrestrial gastropods are more than five times as diverse as their freshwater counterparts, the majority of all land snails derive from a single colonisation event at the base of Stylommatophora.

(4) The distribution of fossil faunas and species diversity is uneven and biased towards northern hemisphere continents. Two-thirds of all fossil species have been described from Europe. On the one hand, this uneven distribution relates to the higher number of long-lived lake faunas, which were particularly common in Europe and which have both high diversity and a better preservation potential. On the other hand, the known distribution may partly be an artifact of a longer and more intense research history in the global north.

(5) Across large spatio-temporal scales, diversification of freshwater gastropods is strongly influenced by the availability of suitable ecosystems that provide stability over extended geological periods, which in turn depends on tectonics and climate. Prime examples are long-lived lakes, which have provided ideal conditions for the taxonomic, phylogenetic, and morphological evolution of gastropods and thus yielded unique biodiversity hotspots. A new term is introduced here to summarise the abiotic and biotic conditions that lead to the ecological requirements facilitating diversification: scale-independent ecological opportunity.

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IX. DATA AVAILABILITY STATEMENT

All data are provided as online Supporting Information.

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XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Fossil species diversity of all freshwater/oligohaline gastropod superfamilies across stratigraphic epochs.

Fig. S2. Fossil species diversity of all freshwater/oligohaline gastropod families across stratigraphic epochs.

Table S1. List of all fossil species-group taxa of freshwater and oligohaline Gastropoda used in analyses.

Table S2. Distribution data in the form of geographic polygons for fossil freshwater and oligohaline Gastropoda.

Table S3. Fossil age data for freshwater and oligohaline Gastropoda.

Table S4. First occurrences of gastropod families containing freshwater taxa in the fossil record.

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